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POPULATION STUDIES OF THE CAVE BAT
(*MYOTIS VELIFER*):
REPRODUCTION, GROWTH, AND DEVELOPMENT

By

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An integral part of the ecology of an animal is the manner in which it successfully adapts to its environment. Under conditions of thermal seasonality in the temperate zones, insectivorous bats have evolved strategies that compress reproduction and development into a relatively short time period in the warm season, when food is abundant and temperature conditions are optimal for rapid growth of young.

Seasonal reproductive patterns of temperate insectivorous bats (including autumn copulation, spring ovulation and gestation, and summer parturition) have been documented for several species. Much of the available information on reproduction has been summarized by Asdell (1964), Barbour and Davis (1969), and Carter (1970). Wimsatt (1945, 1960a) gave a thorough account of breeding behavior, pregnancy, and parturition of several vespertilionids and also discussed aspects of reproduction relating to hibernation (Wimsatt, 1960b, 1969). Orr (1970) summarized studies on growth and development.

There are a number of important studies detailing aspects of natural history, population dynamics and behavior of *Myotis velifer* (J. A. Allen) (Twente, 1955a, 1955b; Tinkle and Milstead, 1960; Tinkle and Patterson, 1965; Dunnigan and Fitch, 1967; and Hayward, 1970). Other important contributions are those of Vaughan

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(1959) on functional morphology and Constantine (1957) on pelage and molt. However, these studies do not assess an entire seasonal cycle, and little is known with respect to the reproduction, growth and development of *M. velifer*. In this study I have considered the seasonal chronology of reproduction and examined factors relating to growth and development in two populations occupying physically and thermally contrasting nurseries in Kansas.

The ecological and geographic distribution of *M. velifer* typically is patchy and extends northward from Honduras into the central Great Plains. The study area lies within the Gypsum Hills and adjacent areas of south-central Kansas. A complete discussion of the study area was given by Kunz (1973). See the appendix for place names, coordinates, and counties of each locality mentioned in text. Of the four races of *M. velifer* currently recognized, the northernmost race is now known as *Myotis velifer grandis* Hayward (1970) and occurs in parts of Texas, Oklahoma and in south-central Kansas. Previously, the name *Myotis velifer incautus* (J. A. Allen) was used for these bats (Miller and Allen, 1928).

Climatically, the study area is typical of the southwestern plains. Most of the area falls within the 0° C January isotherm and above the 26° C July isotherm (U.S. Department of Commerce, Climatological Data). The length of the average frost-free period varies from 180 to 190 days. The last vernal frost occurs in April and the earliest frost in autumn usually is in late September or early October. The summers are long, hot, and dry; it is not uncommon for temperatures of 39° C to prevail for several days. The warmest months are July and August. Winters generally are mild, although temperatures may remain below freezing for short periods. The coldest period usually occurs in February and early March, although this may vary considerably from year to year. Precipitation varies locally and seasonally and months may pass with little measurable amounts recorded. Mean annual precipitation is 16-28 in. (406-711 mm).

Acknowledgments

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METHODS AND MATERIALS

Field studies were begun in March 1968 and continued through January 1971. Data for mark-recovery analyses include all recoveries through June 1970. All bats were marked using size 2b, lipped, aluminum bat bands (U.S. Fish and Wildlife Service, Washington, D.C.). Some bands were color-anodized (blue, green, and red) for marking juveniles occupying different nurseries. Four "seasons," corresponding to Summer (June-August), Autumn (September-October), Winter (November-March), and Spring (April-May), were selected to best represent the seasonal changes in population behavior. Although this scheme does not correspond exactly to the seasonal activity of the entire population, it does represent a general pattern and probably includes most populations in the study area.

Environmental Measurements

Lost Colony and Wilmore were selected for intensive study in order to assess the influence of ambient temperature and relative humidity on reproduction, growth and development. These two nursery roosts, a cave and a barn respectively, were selected mostly because populations of approximately the same size occupy them in the summer. Also, the roosts invite comparative study because their environments contrast sharply with respect to physical and thermal properties.

Temperature and relative humidity recordings were taken in roost areas using seven-day recording hygrothermographs and a Bendix Psychron. Twenty-four hour recordings of micro-roost temperatures (including body-surface temperatures), were obtained using a 12 channel, Model 44, YSI telethermometer with general purpose thermister probes positioned in roost areas at the Wilmore barn. Periodic recordings were made from April through October (Kunz, 1973). Similar attempts were made to measure micro-roost temperatures and body-surface temperatures of bats occupying Lost Colony but these efforts were unsuccessful. Whenever thermisters were positioned in an area that had been occupied by bats they would either abandon that specific site or would move to a different part of the cave. Temperature and relative humidity measurements also were taken at other roosts.

Population Estimates, Age, Sex, and Reproductive Condition

Methods used to estimate population size of active bats depended on the number and size of entrances used by the bats. Where single entrances to caves or buildings were used, flight counts were employed (see Dwyer, 1966; Humphrey, 1971) and this method probably provided the most accurate estimate. Flight counts were not practical at sites with multiple-use entrances; in such situations, estimates were often based on the size of the stained area in a roost, the quantity of the accumulated guano, or number of neonates present after adults had departed. In a few instances, estimates were based on observations of clusters occupying ceiling areas.

Sex ratios were determined mostly from trap samples (Tuttle, ms.) taken at entrances during emergence and return activity, over streams, or by taking hoop-net or hand samples within a roost. The two latter methods were avoided during the nursery period (June-July) in order to reduce disturbance, and were used selectively at other times.

Young bats born in summer could be distinguished from adults at least through August. Generally, after this time, closure of the epiphyseal region of the phalanges occurred and many young bats developed adult-like pelage, and some were nearly equivalent to adults in body weight (Kunz, 1971). After August, age determination was based on the condition of teats in females and size of testes in males. Young females usually have smaller, non-pendulant teats in contrast to those of post-lactating adults, and young males have smaller testes than adults. However, this aging criterion for males becomes less reliable in late September and October when testicular regression occurs in adults.

Reproductive condition of females (pregnancy, lactation, and post-lactation) was determined by palpation. In April and early May pregnant females can not be distinguished from those that may be non-reproductive. In summer, non-pregnant females were considered to be lactating if milk could be extruded from the mammary tissue, or white areas were notably visible beneath the skin. When milk no longer could be obtained, or mammary tissue was visibly pink and undergoing regression, individuals were considered to be post-lactating. Judgments of reproductive activity were based solely on the presence or absence of a discernible fetus in the latter two or three weeks of gestation and the presence of milk in the first week of lactation. When all individuals have given birth, the difficulty of estimating the proportion of reproductive females in the population was compounded by the fact that some females may have aborted in late term or lost their offspring in early days following parturition. These individuals may appear to be non-reproductive upon gross examination so the category is probably appropriate

for them. Reliable estimates of non-reproductive females in a population also are contingent on the fact that they, too, reside in nurseries.

Establishment of a seasonal reproductive pattern for adult males was based mostly on linear measurements of testes and the cauda epididymides from preserved samples. Field observations on the changes in the size and position of testes and epididymides provide a general measure of seasonal activity; however, I think that temporal aspects of the reproductive pattern of adult males can be extrapolated from the pattern observed in preserved specimens.

Growth and Development

Studies of prenatal growth were based on preserved fetuses, which were removed from autopsied females and weighed to the nearest 0.01 gram using a Mettler top-loading analytical balance. Linear measurements of the width and length of the uterine horns and crown-rump length were taken from preserved specimens.

The field methods utilized in studies of post-natal growth were selected primarily to minimize disturbance to nursery colonies. Data obtained from any one nursery were limited by the location and type of structure, the size of the resident colony, and its relative susceptibility to disturbance. Studies at Lost Colony were conducted mostly for the assessment of morphological growth, whereas those at Wilmore were conducted for the purpose of recording behavioral observations.

Preliminary observations at Lost Colony and at other nurseries suggested that an interval from one to one and a half hours was permissible to capture, process, and return young to their roosts before adults returned from foraging. During this period some behavioral observations were made on social organization and age distribution of young within the roost. The procedure of sampling and observing young while adults were foraging was advantageous in reducing disturbance to the colony. However, the recovery rate of known age individuals was low once young became volant. In spite of this disadvantage, the procedure was preferable to sampling bats in the daytime when excessive disturbance to adults may result in high mortality and/or abandonment.

Captures of newborn (or very young) bats were essential for a complete analysis of post-natal growth. Young bats having attached umbilical cords were assumed to be approximately one day old. This assumption has been used by others (see Pearson *et al.*, 1952; Davis, 1969b), although it may not always be valid. When the relative humidity of roosts is high, the umbilical cord may remain attached to a neonate longer than one day. Young bats were sexed, banded, weighed, and measurements of the forearm and fifth finger

were taken. Color-anodized bands were used in roost areas for distinguishing young from adults once the former were fully grown.

At approximately 10-day intervals, newly captured neonates and young that had been previously marked were captured and processed. By the beginning of the fourth week, several young that had been marked in the first period had become volant. Throughout the summer unmarked samples of young bats that were trapped at colony entrances or in roost areas were processed as described above.

Periodic samples of unmarked young corresponding to sizes of known-age bats, were collected from several different colonies. These bats were killed and preserved in 10 percent formalin for studies of pelage, dentition, and food consumption. Drawings of wing areas were made before preservation for the purpose of studying age-related changes in wing-loading. Wing areas were traced on paper in the field and surface area determinations were made following the methods described by Davis (1969a). Linear and wing-area measurements, were taken using a metric dial caliper (0.1 mm) and a polar planimeter (0.1² inches), respectively; the latter measures were converted to metric units (cm²).

Binoculars (7 x 35) were used for making observations at Wilmore. At this site ambient light conditions were usually sufficient for making diurnal observations from a distance of approximately five meters without noticeably disturbing the colony.

On periodic visits to each nursery, I examined areas beneath roosts for evidence of juvenile mortality. However, this search was hindered at Lost Colony because small young became buried in the wet guano after falling to the cave floor. This problem was not encountered at building nurseries where guano usually dried rapidly under conditions of low relative humidity.

Growth Analysis

A FORTRAN program, fitting properties of the von Bertalanffy growth model applicable to mark-recovery data (Fabens, 1965), was used in the analysis of post-natal growth. The only basic input requirements of this program are sets of linear or weight data (arranged as paired measurements, and corresponding capture intervals that need not be equal) and a separate input that includes linear size or weight of some known-age individuals (preferably those taken at or near birth). In the analysis that follows, linear growth is expressed by the general formula $X = a(1 - be^{-kt})$ and weight by the formula $W = [a(1 - be^{-kt})]^3$, where X represents the computed length of the forearm or fifth finger, and W is the 2/3 power of the body weight. The quantities a , b , and k in both equations are parameters: a is a measure of the asymptotic size; b is a measure related to the size of the animal at birth; and k is a measure of the intrinsic rate of growth. The values e and t represent the base of the natural logarithm and the number of days of growth, respectively.

A thorough account of the mathematical and physiological theory of the model was presented by von Bertalanffy (1960); he cautioned that at present quantitative analysis of growth in mammals must be considered provisional. Laird *et al.* (1965) and Laird (1966) used models based on the Gompertz equation for studying growth of body weight in mammals. However, von Bertalanffy argued that models based on this equation are not only unsuitable for analyses of linear measurements but also lack a physiological basis for application to study of growth.

Curve-fitting of growth data is useful to summarize data for descriptive purposes. If a growth curve is derived from a theoretical model, so that parameters have some additional meaning, independent investigations then can be conducted to test the theory on which the model is based. The von Bertalanffy growth curve of the decaying exponential type (von Bertalanffy, 1960) has been derived from a model that has physiological significance and provides parameters that are useful for independent testing. The underlying assumption of this model is that growth, in the biological sense, is intimately related to metabolism and is characterized by the highest rates in the early stages of development, decreasing exponentially with time.

RESULTS

Nursery Roost Environments

Nursery "caves" seldom showed significant daily fluctuations in temperature or relative humidity. Hygrothermograph recordings taken at Lost Colony in late spring and summer 1969 revealed little daily change in ambient temperature or relative humidity. A representative record in the second week of July showed that the cave temperature remained near 20° C and the relative humidity near 100 percent (Fig. 1). Periodic measurements of temperature and relative humidity in the nursery area at the National Gypsum Mine suggest a similar pattern. Much of the gypsum substrate becomes saturated with ground-water following spring and early summer rains at these sites. The accumulation of this water, the presence of seasonally intermittent streams or standing water, and the relatively low air circulation in summer reduce evaporative conditions and contribute to the high relative humidity.

Building nurseries, in contrast to cave nurseries showed marked daily variations of temperature and relative humidity. A comparison of temperature recordings and relative humidity at Lost Colony and Wilmore in the second week of July (Fig. 1) demonstrates these striking differences. In this period temperatures at Wilmore varied from 25-35° C, and relative humidity ranged from 40-100 percent. Because Wilmore was occupied by spring transient and a resident summer population, the recordings shown in figure 2 were selected to depict the roost conditions during this period. It is clear that bats

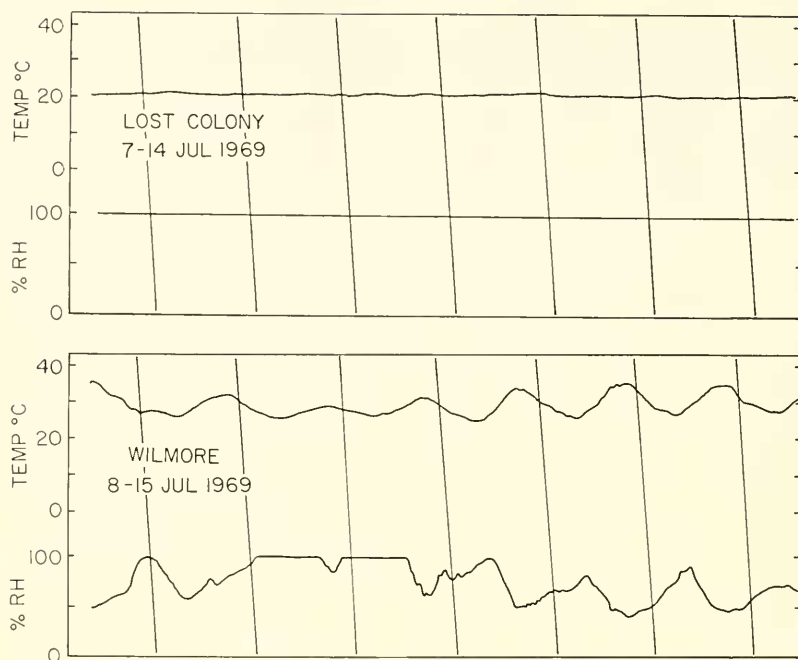


FIG. 1. A comparison of hygrothermograph records during the nursery period (second week of July) at Lost Colony and Wilmore. On both records the temperature measurements (upper) and relative humidity measurements (lower) represent ambient conditions in the colony irrespective of the thermal influence or vapor pressure changes brought about by the presence of the bats. The diagonal lines indicate the 2400 hour (midnight) of each day.

occupying this roost potentially were exposed to widely fluctuating conditions. There is a general seasonal pattern of increasing mean ambient temperatures and decreasing relative humidity from early spring to late summer.

Environmental fluctuations may vary considerably depending on the physical structure of the roost, the location of the building or cave with respect to topography, surrounding vegetation, and the facing direction of the entrance. Ambient temperature in small buildings usually fluctuated more than in large structures. Nursery sites in caves, in contrast to those in buildings, were usually located in areas where little, if any, light penetrated beyond the entrance area. In most buildings, however, light was sufficiently bright during parts of the day to permit observation without the use of artificial sources. At Lost Colony and the National Gypsum Mine no light was evident in the nursery areas but at Wilmore bats occupied dimly lighted areas and the darkest areas were not occupied.

Clustered bats modify the microclimate of their nursery roosts. Tendencies of bats to cluster, coupled with the physical features of

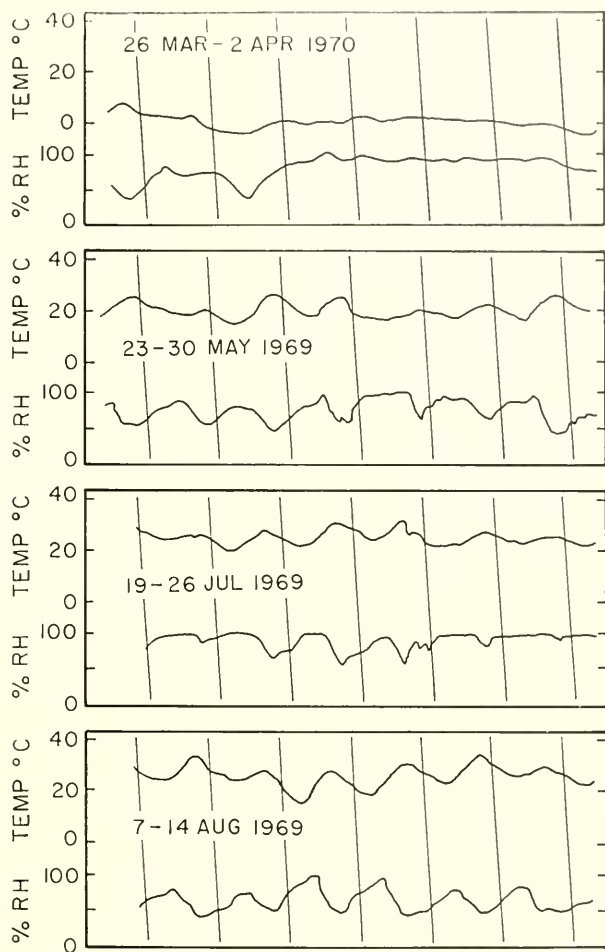


FIG. 2. Hygrothermograph records showing seasonal patterns of ambient temperature and relative humidity at a barn occupied by transient and nursery populations of *M. velifer*. The diagonal lines indicate the 2400 hour (midnight) of each day.

the roost, combine as important factors in maintaining high roost temperatures. Microenvironmental temperatures recorded in roosts at Wilmore in late June often reached daytime levels exceeding 35°C (Fig. 3). To assess the effect of bats on their roost microclimate, temperature differentials between test probes and control probes were determined (see insert Fig. 3). I have assumed that these differences represent the thermal influence that bats had on their roost microclimate. On 29-30 June these differences varied from 4-

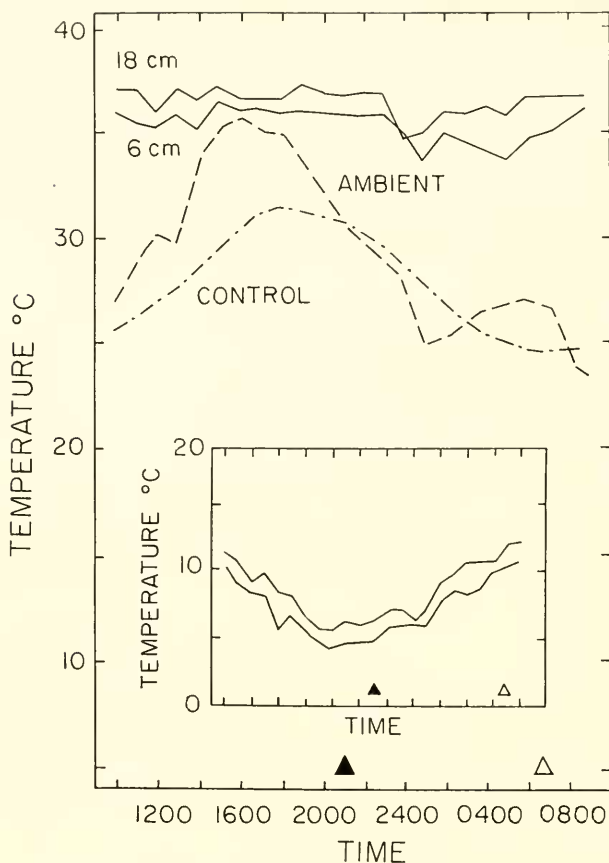


FIG. 3. Microenvironmental temperatures recorded at the Wilmore nursery on 29-30 June 1969 (after most females had given birth). Data are based on hourly temperatures recorded along a vertical gradient in a joist crevice from thermisters positioned at 6 and 18 cm from the ceiling (see Kunz, 1973 for further explanation). One daily record of a control probe (6 cm) and the outdoor ambient temperature are shown for comparison. The insert shows temperature differentials between control sites (bats absent) and test sites (bats present). The solid and open triangles at the bottom of the figure denote sunset and sunrise time, respectively.

12° C depending on the time of day and the number of bats present at any one time. Much of the loft floor at Wilmore was covered with loose straw and broken hay bales to a depth ranging from two to 40 centimeters. The accumulated litter may have been important in providing insulation by trapping heat that was generated by bats roosting on the joists supporting the loft floor.

The daily and seasonal fluctuations of relative humidity in building roosts also were subject to modification by bats. In spite of the pattern of relative humidity recorded in the Wilmore barn (Figs. 1 and 2), the presence of clustered bats in the daytime tends to modify the vapor pressure in roosts when, otherwise, it is low. In June and July 1969 and 1970, roosts were examined periodically after adults had departed to feed. These observations revealed that the wood substrate of joists on which the bats roosted was saturated with urine. Instruments were not available that would permit remote micro-determinations, but measurements of relative humidity using a Bendix Psychron positioned at the opening of joist crevices revealed substantially higher readings than from the hygrothermograph recordings taken in open areas near the joist crevice. It is quite probable that as these wood joists become saturated during periods of occupancy, increases in vapor pressure become comparable to the 100 percent saturation recorded in cave nurseries.

In early spring, the thermal environment at Lost Colony appeared to be unsuitable for occupancy; temperatures varied from a low of 8° C in mid-April to 13° C in mid-May, and little daily variation was evident. These temperatures were considerably lower than those recorded at other spring roosts and that were occupied by transient populations (Kunz, 1971). When individuals first arrived at Lost Colony in early May, they usually selected the warmest sections available. In contrast, Wilmore was subjected to the environmental fluctuations of the outside environment. In early spring, roost temperatures occasionally dropped below 0° C but by May daily highs reached 30° C (Fig. 2).

Adult Sex Composition of Nursery Roosts

Adult male *M. velifer* accompany females to nursery roosts; this phenomenon is apparently uncommon in other members of the genus. The sexes occur in nearly equal numbers in spring transient roosts and in nurseries until parturition begins (Table 1). Monthly comparisons of the proportion of adult sexes occupying Lost Colony and Wilmore showed that the males occupying these two sites declined measurably in May and June. Proportionately fewer males remained in the barn at Wilmore from May through August than occupied Lost Colony during the same period.

Samples of bats taken at the National Gypsum Mine in July and August, 1969, revealed that a comparatively large proportion of males occupied this site. Here, many males occupied cool caves and were solitary or roosted in small groups. On 19 August several bats were found scattered throughout the mine at considerable distances from the nursery area; of 39 individuals captured, 38 were adult males. A trap sample on the same date during emergence activity yielded 406 bats, of which 296 were males.

TABLE 1. Seasonal comparisons of adult male *Myotis velifer* occupying nurseries at Lost Colony (cave) and Wilmore (barn).

Month	Lost Colony				Wilmore			
	Number of samples	Pooled N	Males	Percent males	Number of samples	Pooled N	Males	Percent males
Mar	—	—	—	—	1	49	23	47.0
Apr	1	4	2	50.0	1	112	51	45.6
May	2	216	106	49.0	4	304	87	28.6
Jun	4	696	106	15.2	2	343	28	8.2
Jul	3	574	194	33.8	5	305	24	7.9
Aug	4	687	137	20.0	4	93	10	10.7
Sep	3	241	48	20.0	2	15	2	13.3
Oct.	1	68	65	95.4	1	20	20	100.0

Reproduction

MALES

Testes and Epididymides.—Seasonal changes in size of testes and epididymides of adults show that testes increase in size following departure from hibernacula with maximum hypertrophy occurring in late August (Fig. 4). These observations concur with those of Krutzsch (1961) and Hayward (1970) based on samples from Texas and Arizona, respectively. Increase in the size of testes corresponds to the period of spermatogenesis in summer reported for other vespertilionids (Wimsatt, 1960b, 1969). In early autumn when testes decrease in size, the epididymides become distended with spermatozoa. Maximum engorgement of the cauda epididymides occurs in October and is followed by a decrease in size throughout the winter. Testes are abdominal throughout hibernation and early spring, but in mid-summer (July) they descend into the pigmented sheaths adjacent to the tail in the uropatagium.

FEMALES

Age at Sexual Maturity.—Female *M. velifer* apparently reach sexual maturity in their first year of life. Thirty-nine females were recovered from 21 May through 21 June 1970, that had been marked as juveniles in the preceding summer; all were either pregnant or lactating. It was not determined whether or not yearling females are inseminated in spring or at other times.

Ovulation and Fertilization.—Wimsatt (1944, 1945) suggested that ovulation in *M. lucifugus* probably occurs between the time of departure from hibernation and arrival at nurseries in spring. If fertilization in *M. velifer* occurs at this time, then this would include the period from late March to late April for populations in this study. In 1970, some females had already departed from hiber-

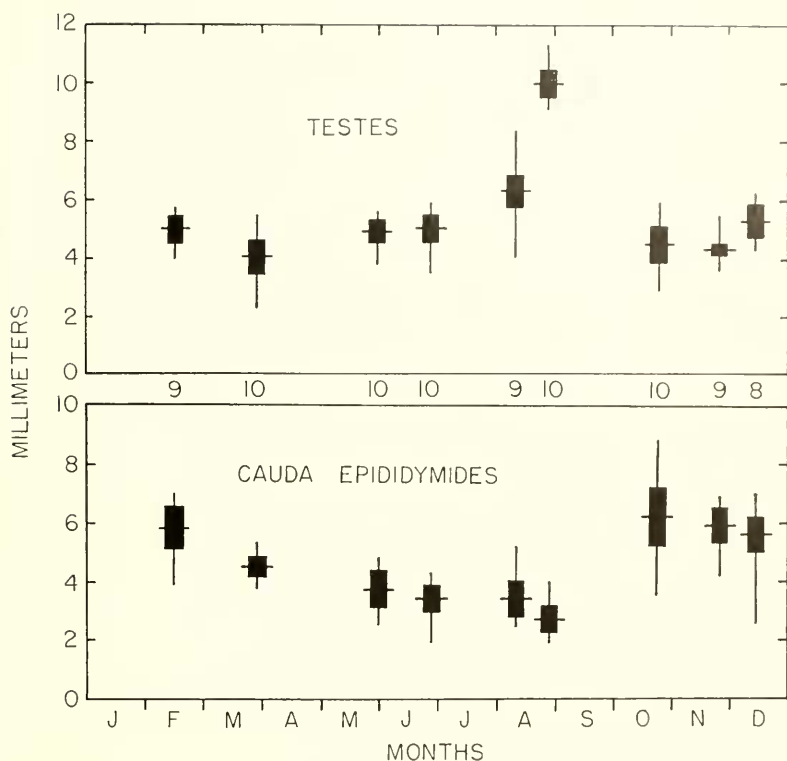


FIG. 4. Seasonal changes in size of testes and cauda epididymides of adult male *M. velifer*. Dice grams indicate mean, range and 2 SE. Sample sizes are shown between the two graphs.

macula and had arrived at spring roosts by 25 March, although the median departure date from hibernacula was estimated to be mid-April (Kunz, 1971).

Gestation and Prenatal Development.—The means for length and width of the right uterine horn (Table 2) are plotted to portray the general period of gestation and pattern of prenatal growth (Fig. 5). Prenatal growth follows a sigmoidal pattern with a characteristic lag phase in the early stages. Throughout this early period of growth, the length and width of the uterine horn were nearly proportional. Most of the growth up to this time mainly reflected the increase in the size of the uterus, the placenta, and extraembryonic membranes. Once these tissues are well developed, embryos grow rapidly as evidenced by their elongation, change in the relative proportions of the linear dimensions of the uterine horn, and increase in embryo size and weight. Mean weight of the fetus at birth was approximately 3.0 grams; on 29 May, about three weeks before

TABLE 2. Prenatal growth of *Myotis velifer*, where growth is expressed as the length and width (± 0.1 mm) of the right uterine horn, weight (± 0.01 gm) and crown-rump length (± 0.1 mm) of the fetus (means \pm SE and ranges are given).

Date	N	Length of right uterine horn (mm)			Width of right uterine horn (mm)		
		\bar{x}	SE	Range	\bar{x}	SE	Range
24 Apr	12	2.6	0.14	(1.9- 4.0)	1.9	0.09	(1.5- 2.7)
8 May	12	4.0	0.25	(2.9- 6.3)	3.6	0.29	(2.3- 6.1)
29 May	9	12.8	0.99	(9.1-17.4)	10.1	0.89	(6.4-14.4)
11 Jun	15	21.4	0.41	(18.8-24.1)	13.6	0.18	(12.5-14.8)
16 Jun	11	23.9	1.92	(16.3-26.4)	15.8	0.61	(14.5-16.9)
20 Jun	8	23.7	0.94	(20.4-28.0)	16.1	0.51	(14.0-18.2)

Date	N	Weight of embryo (gm)			Crown-rump length (mm)		
		\bar{x}	SE	Range	\bar{x}	SE	Range
24 Apr	12	---	---	---	---	---	---
8 May	12	---	---	---	---	---	---
29 May	9	0.43	0.073	(0.05-0.73)	10.3	0.98	(6.2-15.9)
11 Jun	15	1.66	0.068	(1.20-2.25)	20.7	0.43	(17.9-23.5)
16 Jun	11	2.31	0.176	(1.10-3.30)	23.6	0.78	(16.4-27.1)
20 Jun	8	2.80	0.251	(1.90-3.92)	23.1	0.72	(20.4-26.0)

parturition, mean embryo weight was 0.43 grams, representing only 14.3 percent of the fetal weight at birth. It is clear from these data that most of the prenatal growth occurs in the last three weeks of gestation.

The sex ratio of fetuses did not differ significantly from unity. Before late May sex determination was not possible by external macroscopic examination of the fetus. Sex determinations made on and following 29 May revealed 26 males and 22 females (Chi-square, 0.31, $P > 0.05$). The sexes of five fetuses taken on 29 May could not be determined owing to their exceedingly small size and relatively underdeveloped condition.

Samples from various nurseries were taken from late May through August to assess the reproductive condition of females. The data summarized in table 3 represent the number and percentage of pregnant, lactating, and post-lactating females captured in this interval. Data for Lost Colony and Wilmore are plotted separately (Fig. 6) and form the basis for the following discussion. A median parturition date was estimated when 50 percent of the reproductive females sampled at each location had produced young. In 1969 this date was estimated to be on 21 June both at Lost Colony and Wilmore.

If one assumes that 15 April was the median date for fertilization and 21 June for the median parturition date, then the gestation period for *M. velifer* is approximately 67 days. If individuals that

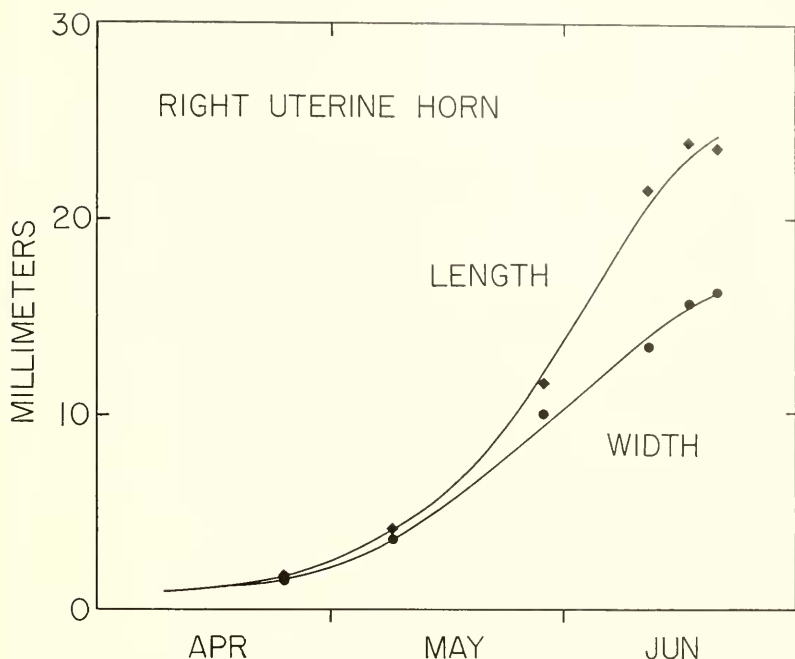


FIG. 5. Period of gestation and pattern of prenatal growth of *M. velifer* expressed as the mean increase in length and width of the right uterine horn (also see table 2).

arrived at Wilmore on 26 March were indeed pregnant and parturition began soon after 11 June, this would suggest a gestation period of approximately 77 days, assuming that these individuals were the first to give birth. Based on the available data, the most reliable estimate probably lies somewhere between 60 and 70 days. Wimsatt (1945) estimated that the gestation period in *M. lucifugus* ranged from 50 to 60 days and Pearson *et al.* (1952) reported the gestation period for *Plecotus townsendii* in California as 56 to 100 days.

Parturition.—The parturition period at Lost Colony and Wilmore extended over a period approximating four weeks in 1969 and corresponded closely to the range of departure dates from hibernacula. Periodic examination of the number of young occupying these two nurseries in June and July supported the contention that most of the young are born within a short period. Nearly 80 percent of the births occurred in a two-week period from 14 to 28 June. On 8 June 1969 no young were present in the nursery at Lost Colony, although approximately 100 and 400 neonates were present on 16 and 17 June, respectively. These data indicate that approximately 300 young were born within a 24-hour period between the nights of 16 and 17 June. Ten days later, on 27 June, there were nearly 4500

TABLE 3. Seasonal changes in the reproductive condition of adult female *Myotis velifer* occupying nursery colonies in Kansas.^a

Date	Pregnant		Lactating		Post-lactating		Location
	N	Percent	N	Percent	N	Percent	
22-23 May 1970	48	100.0					Wilmore
28 May 1969	230	100.0					Englewood ^b
28-29 May 1969	69	100.0					Wilmore
30-31 May 1969	96	100.0					Lost Colony
8-9 Jun 1969	124	100.0					Lost Colony
9-10 Jun 1969	10	91.0	1	9.0			Nat'l Gypsum Mine
10-11 Jun 1970	42	100.0					Wilmore
16-17 Jun 1969	83	84.7	15	15.3			Lost Colony
18 Jun 1969	56	96.5	2	3.5			Nat'l Gypsum Mine ^b
18-19 Jun 1969	51	76.2	16	23.8			Belvidere
19-20 Jun 1970	147	66.6	68	33.4			Wilmore
21 Jun 1970	266	74.7	90	25.3			Lost Colony ^b
21-22 Jun 1970	45	50.0	45	50.0			Nat'l Gypsum Mine
27-28 Jun 1969	13	12.0	95	88.0			Lost Colony
28-29 Jun 1969	7	7.0	92	93.0			Wilmore
29-30 Jun 1969			210	100.0			Wilmore
7-8 Jul 1969			122	100.0			Lost Colony
8-9 Jul 1969			107	100.0			Wilmore
9-10 Jul 1969			27	100.0			Wilmore
18-19 Jul 1969			153	100.0			Lost Colony
19-20 Jul 1969			10	100.0			Wilmore
27-28 Jul 1969			78	74.2	27	25.8	Lost Colony
28-29 Jul 1969			5	83.4	1	16.6	Wilmore
31 Jul 1969			101	60.4	66	39.6	Double Entrance S ^b
31 Jul —							
1 Aug 1969			196	77.5	57	22.5	Protection
6-7 Aug 1969			42	37.5	70	62.5	Lost Colony
7-8 Aug 1969			3	15.7	16	84.3	Wilmore
8-9 Aug 1969			6	10.9	49	89.1	Wilmore
10 Aug 1969			31	14.9	177	85.1	Lost Colony ^b
16-17 Aug 1969					93	100.0	Lost Colony
17-18 Aug 1969					18	100.0	Wilmore
19 Aug 1969			1	0.4	210	99.6	Nat'l Gypsum Mine
20 Aug 1969					189	100.0	Protection ^b
27-28 Aug 1969					11	100.0	Wilmore
31 Aug —							
1 Sep 1969					136	100.0	Lost Colony

^a Non-reproductive females were excluded because they usually represented less than one per cent of any sample.

^b Roost sample.

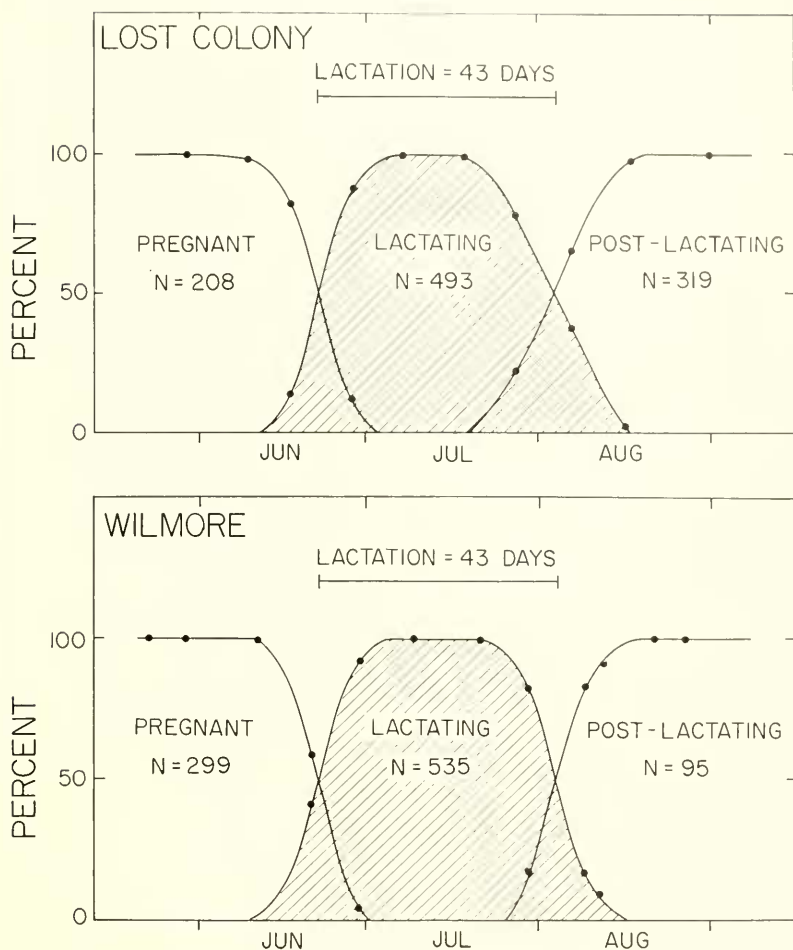


FIG. 6. A comparison of the summer reproductive patterns of female *M. velifer* expressed as the percentage of pregnant, lactating, and post-lactating individuals sampled at Lost Colony and Wilmore. The median parturition date is indicated when 50 percent of the reproductive females had already produced young. The interval between the median parturition date and the median cessation date of lactation represents an estimated individual lactation period.

young ranging from one day to nearly two weeks of age. If 50 percent of the young were born by 21 June this would mean that in the four-day period from 18 to 21 June, an average of more than 500 young were born per day. Similar observations were made at Wilmore. A trap sample taken at an entrance to the National Gypsum Mine on the night of 22 June 1970 (45 pregnant and 45 lactating females) revealed a comparable median parturition date.

Some authors have suggested that yearling females of some spe-

cies give birth later in the season than older bats (see Griffin, 1940; Pearson *et al.*, 1952; Davis and Hitchcock, 1965). To test the null hypothesis that there was no difference in parturition dates of yearling or adult *M. velifer*, I examined females that had been marked at Lost Colony and Wilmore in 1969 and recovered there between 19 and 21 June 1970. Of 22 adults and 28 yearlings recovered in this period, six adults (27.2%) had already given birth or were lactating and only four yearlings (14.8%) had given birth. A *t* test for the equality of these two percentages was non-significant ($t=1.14$, $P>0.05$) thereby supporting the null hypothesis.

Actual parturition was not observed in the field, although studies conducted in captivity (unpublished observations) concur with those of Twente (1955b) and Wimsatt (1945, 1960a) for *M. velifer* and *M. lucifugus*, respectively. Fresh paper was placed beneath nursery areas at Wilmore in an attempt to determine if the placentae were dropped or eaten. The fact that few were found beneath roosts occupied by several hundred young is circumstantial evidence that placentaphagia is practiced by *M. velifer*.

Nursing.—Soon after parturition, females begin to nurse their young. A noticeable decrease in the intensity of audible vocalizations was observed between 0800 and 1000 and again between 1500 and 1800 in the Wilmore barn. I have interpreted this to indicate two nursing periods; one follows the return of females in morning and another occurs in late afternoon. The evidence is circumstantial, but it seems reasonable that a reduction in vocalization would occur when young are nursing. Also, between 1100 and 1300 hours I observed a large proportion of adult females occupying open-faced joists adjacent to the areas mostly occupied by both young and adults at other times. Based on samples of young and the amount of milk found in their stomachs during the daytime, Davis *et al.* (1962) suggested that female *Tadarida brasiliensis* have two daily nursing periods.

In the first weeks following parturition, many female *M. velifer* return to their young within an hour or two after emergence; whether or not nursing takes place at this time was not established. When females departed in the evening, little milk could be expressed from the mammary tissue, whereas females returning to the roost after 0400 appeared to have fully distended mammary glands.

Little is known concerning the length of time females nurse their offspring. The lactation period may be approximately 43 days (or six weeks) if one assumes that the time interval between the estimated median parturition date and the median cessation date of lactation represents the average for an individual (Fig. 6). Most young begin to forage well before the age of six weeks (see section on Growth and Development). And, evidence based on captures of

TABLE 4. Annual reproductive effort of female *Myotis velifer*.

Date	Females	Reproductive females ^a	Percentage of reproductive females
20-31 May	443	443	100.0
1-10 Jun	180	177	98.4
11-20 Jun	242	240	99.2
21-30 Jun	861	861	100.0
<i>Total</i>	1,726	1,721	99.9

^a Pregnant and lactating females (table 3) sampled from late May through June; reproductive activity (pregnancy and lactation) was determined by palpation.

foraging young suggests that they continue to nurse after they have become volant.

Reproductive effort.—Yearling and adult females captured at all nurseries were pooled at 10-day intervals from 20 May through 30 June for an analysis of annual reproductive effort (Table 4). These data, coupled with the fact that only a few barren females were found, indicate that most adult female *M. velifer* in the population are reproductive and also that females reach sexual maturity in their first year. If non-reproductive females remain solitary or occupy other sites separate from nurseries then the annual reproductive effort of 99.9 percent may be an overestimate. Some pregnant females, which had aborted or lost their offspring at birth, may have been considered as non-reproductive individuals upon external examination. If these individuals were counted as non-reproductives, but in reality had been parous, then the overestimate resulting from the possibility of a greater proportion of non-reproductives at other locations is offset.

Growth and Development

GROWTH PATTERNS

Growth curves and descriptive parameters based on 90 paired records for body weight, forearm, and fifth finger are shown in figure 7. Relative growth is expressed as the percentage of body weight and size of adults from samples taken in mid-August (Fig. 9). For linear measures (forearm and fifth finger), relative growth is based on curves shown in figure 7. Relative changes in body weight were based on sample means shown in figure 8 and tables 5 and 6. Data for both sexes were combined in the analysis because there were no significant differences in weight or linear measures in the early stages of post-natal development. Unless otherwise indicated, linear measurements are based on values extrapolated from the computed curves. It should be understood that these curves repre-

TABLE 5. Body weight, wing size, and wing-loading of known age, pre-volant juvenile *Myotis velifer* (means and standard errors).^a

Age (days)	N ^b	Forearm (mm)		Fifth finger (mm)		Weight (gm)		Wing area (cm ²)		\bar{x} wing loading (gm/cm ²)
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	
1-2	89	17.0	0.09	19.0	0.11	3.2	0.03	10.75	0.53	.298
11-12	26	30.5	0.21	32.5	0.26	7.6	0.12	31.09	0.89	.245
21-22	26	41.3	0.29	48.5	0.39	10.6	0.21	82.58	1.38	.128

^a Samples are based on recaptured individuals that were initially marked when approximately one to two days old.

^b Each sample size for wing area was 10.

sent best fit approximations to the observed data, and that variation due to errors in measurement and stochastic properties are inherent.

Bats that had been marked as neonates seldom were recovered in the roost area more than twice. Of 175 neonates marked at Lost Colony in 1969, 90 recoveries of 64 individuals were made. Loss of bands may account for a low recovery owing to the fact that bands may slip over the wrist of neonates before wing dimensions reach sufficient size to hold them in place. However, only two lost bands later were found beneath the roost. Apparent "loss of bands" may occur if mothers move their young following disturbance (see Roer, 1968; Fenton, 1969a; Davis, 1970), and account for a low recovery of non-volant young. After young became volant, the probability of recovering them (while foraging or at entrances) is even lower.

On the day of birth the calculated lengths of the forearm and fifth finger were 16.0 and 18.0 mm, respectively. (The forearm measured approximately 34% of the adult size, whereas the fifth finger was only 29%.) By three weeks of age the forearm exceeded 80 percent of the adult size and by the fourth week, when most of the young had begun to forage, the forearm (43.0 mm) had reached 90

TABLE 6. Seasonal changes in body weight of volant, juvenile *Myotis velifer* (means and standard errors).

Date	Males				Females		
	N	Body weight		SE	N	Body weight	
		\bar{x}	SE			\bar{x}	SE
18 Jul 1969	17	10.4	0.26		16	10.4	0.34
27 Jul 1969	49	10.7	0.12		58	10.7	0.11
6 Aug 1969	59	9.8	0.11		40	10.2	0.15
16 Aug 1969	34	10.2	0.13		38	10.4	0.14
31 Aug 1969	36	11.8	0.11		53	11.9	0.09
7 Sep 1969	35	12.0	0.11		52	12.4	0.07
18 Oct 1969 ^a	55	14.7	0.17		----	----	----
18 Oct 1969	30	15.3	0.25		----	----	----

^a Taken in a hibernaculum.

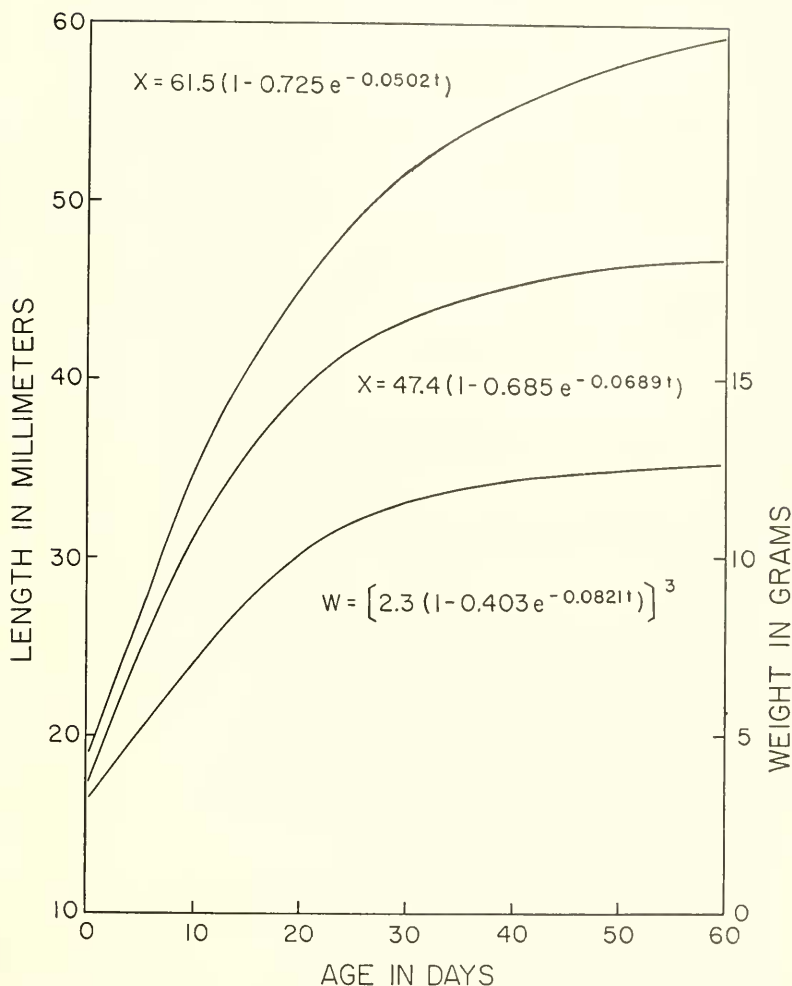


FIG. 7. Growth of juvenile *M. velifer*. The growth curves from top to bottom are fifth finger, forearm, and body weight, respectively. The growth equation for linear measures is expressed by the general formula $X = a(1 - be^{-kt})$ where X is the length in millimeters and t is the number of days of growth. The growth equation for body weight is expressed by the general formula $W = [a(1 - be^{-kt})]^3$, where W is the $2/3$ power of body weight, and t is the number of days of growth. The quantities a , b , and k in both equations are parameters— a , a measure of the asymptotic size; b , a measure related to the size of the animal at birth; k , a measure of the intrinsic rate of growth, and e , the base of natural logarithms.

percent of adult size. In contrast, the fifth finger did not reach an equivalent proportion until the fifth or sixth week. By the time young were 60 days old (approximately mid-August for most) the forearm and fifth finger had reached 98 and 96 percent of adult size,

respectively. The fifth finger, as well as other digits, probably continues to grow at least until late August or early September. This corresponds to the time that closure of the phalangeal epiphyses becomes evident in field examinations. The asymptotic size for the forearm (47.4 mm) and fifth finger (61.5 mm) was reached in approximately 70 days. These calculated values for asymptotic size may be slightly larger than adult means although they do fall within the ranges for the forearm (43.6-48.6) and fifth finger (57.3-62.5) recorded from recently killed and live specimens. Linear measurements based on live individuals are slightly larger than those recorded from dried specimens; for comparison see measurements of *Myotis velifer* recorded for preserved specimens from Kansas by Hayward (1970).

Absolute growth rates for the forearm and fifth finger are shown in table 7. Ten-day intervals were selected to depict relative changes in growth over the 60-day period. In the first 10 days, growth of the forearm and fifth finger was nearly linear. Average increases of 1.56 and 1.71 millimeters per day for the forearm and fifth finger, respectively, can be noted; growth rates in the subsequent 10-day intervals were measurably less.

The computed growth curve for weight was compared with samples of body weights taken at intervals throughout the growth period (Fig. 8). It is evident that the computed curve only represents a general trend and that actual changes in weight after young became volant were obscured in the process of curve fitting. For this reason, relative changes in body weight (Fig. 9) were based on data presented in figure 8. The estimated weight of young at birth is 3.0 grams, approximately 25.8 percent of the weight of post-parturiant females. This value differs slightly from the mean (3.2 gm) shown in table 5, although the discrepancy can be accounted for by the fact that this sample included some individuals that may have been older than one day. By the time individuals were one week old they had reached 50 percent of their adult weight; at three weeks of age they exceeded 85 percent of adult weight. Increases in body weight

TABLE 7. Absolute growth rates of the forearm and fifth finger of *Myotis velifer* expressed in mm/day at ten-day intervals.^a

Age interval (days)	Forearm (mm)	Fifth finger (mm)
1-10	1.56	1.71
11-20	0.81	1.07
21-30	0.34	0.64
31-40	0.21	0.39
41-50	0.10	0.23
51-60	0.05	0.14

^a Rates were computed from data on growth curves shown in figure 7.

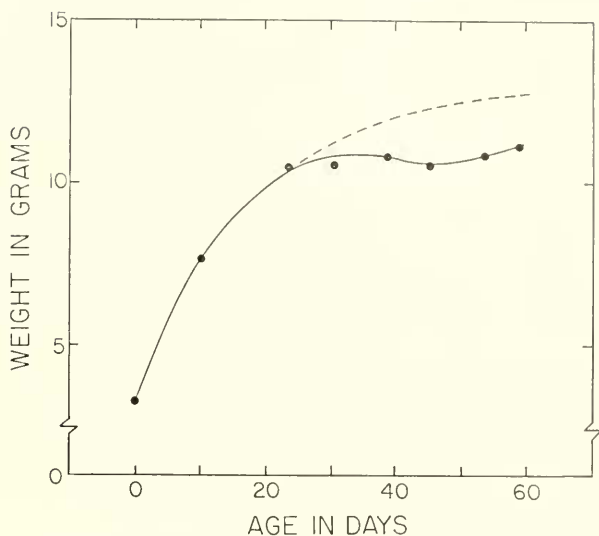


FIG. 8. A comparison of the calculated and realized increase in body weight of juvenile *M. velifer*. The realized increase in body weight is shown by the solid line (closed circles) and represents an eye-fit construction based on sample means (see table 6). The predicted pattern (which includes the dotted line in addition to the early phase of the realized increase) was computed from mark-recapture data using the von Bertalanffy growth analysis. See figure 7 and text.

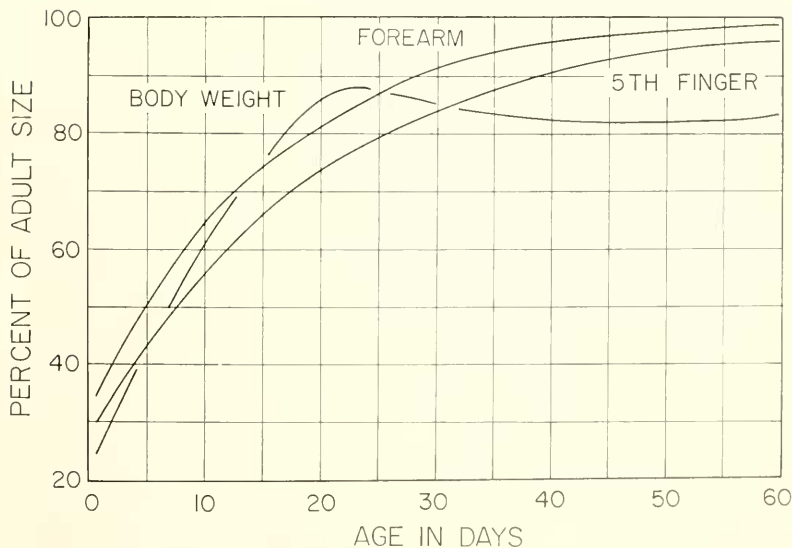


FIG. 9. Growth of juvenile *M. velifer* expressed as the percentage of mean body weight, forearm, and fifth finger of adults taken in mid-August.

were nearly linear for the first three weeks. Based on data in table 5, absolute increase in body weight in this period was 0.36 grams per day. By the fourth week, when most young were foraging, body weight decreased and then stabilized between 82 and 86 percent of the adult weight; subsequent increases were not evident until fat deposition began in late August.

PHYSICAL DEVELOPMENT

Skin and Pelage.—At birth the body is pink, but the wings, interfemoral membrane, distal portion of the ears, and the anterior facial regions are pigmented (pale to dark brown). Short, whitish hairs are scattered over the dorsum, but the most densely haired region is at the base of the interfemoral membrane. Short scattered hairs also are present on the venter but are comparatively shorter and less dense than those on the dorsum. The facial vibrissae and hairs on the feet are relatively well developed.

At the age of one week the hairs on the dorsum have increased in length and density and are brownish gray in color; the longest and densest hairs still are located at the base of the interfemoral membrane. Hairs on the venter are whitish-gray, although still relatively short and sparse. Although skin on the venter remains pink, some areas on the dorsum are lightly pigmented and appear brownish. The vibrissae and hairs on the feet have become increasingly long and stiffened.

By two weeks of age the dorsum is almost completely covered with short, dense, brownish-gray pelage; the hair on the venter also has increased in length and density. Little change is evident in the amount of pigmentation of the membranes, although the skin on the forearm is paler and more adult-like in appearance. The skin on the venter remains pink, but the dorsal skin has become increasingly pigmented and now appears bluish-gray.

At the age of three weeks the hair on the dorsum has become distinctly bi-colored, characterized by a dark brown basal portion and pale brown terminal part. The hairs on the venter are whitish-gray and the skin has darkened. By four weeks the skin on the dorsum is again pink in color, and the pelage is plumbeous in appearance and characterized by a dense, dark undercoat and longer overhairs. The hairs of the venter also are bi-colored, with a dark gray base and a whitish-gray terminal portion; the skin of the venter remains darkly pigmented.

Between the ages of three and four weeks the pelage of some individuals becomes faded. By late July or early August the bi-colored appearance is no longer recognizable and the pelage also appeared to be less dense than when individuals first became volant.

By the time juveniles have become nutritionally independent (at

approximately six weeks), a juvenile molt is initiated. Although this molt extends from early August through late September, only a few individuals have actually begun to molt by the first week of August. The initiation of molt is characterized by a darkening of the skin. Darkening occurs first on the dorsum and then on the venter; replacement of dorsal pelage usually was well underway before the ventral skin darkened. Of 288 individuals examined in mid-August, 130 (45%) showed some sign of molt; by late August some had nearly completed molt, but others had only begun. By the third week of September the pelage of many juveniles was indistinguishable from that of adults.

Dentition.—At birth, *M. velifer* may or may not have a full complement of deciduous dentition. Maximum development of deciduous teeth usually was reached in the first week. Loss of these teeth began at the age of 10 to 12 days; concurrently, some permanent teeth began to erupt lingual to the deciduous dentition. The general description, sequence of loss, and eruption in *M. velifer* generally follow that reported by Fenton (1970) for *M. lucifugus*. By the time individuals were four weeks old all permanent teeth had erupted, although teeth were not well developed until the age of seven to eight weeks.

INFANT SOCIAL BEHAVIOR

The social organization of neonates apparently is influenced by their physical development, motor coordination, and sensory capacity. Young *M. velifer* have relatively poor motor coordination in the first few days after birth and movements in the roost are restricted. Observations made after adults had departed suggest that the smallest young (presumably the youngest) do not move from areas where they apparently have been left by their mothers. By the time young were approximately two days old, their motor coordination had improved considerably inasmuch as most could crawl rapidly over the roost substrate.

Following evening departure of the mothers, young (those older than two days) usually formed dense clusters along natural crevices comprising the roost substrate. In contrast, the smallest (youngest) bats remained scattered, and made little apparent effort to join the clusters of older bats. As an experiment to test the mobility and social instinct of young bats, a number of individuals judged to be more than two days old were moved from clusters which they occupied. Within a few minutes most of these bats returned to a nearby cluster (not necessarily the one from which they had been removed). In contrast, bats that were approximately one day old and displaced from their site of occupancy made little or no attempt to move except to establish a firmer grip on the substrate.

MATERNAL-INFANT RELATIONSHIP

Apparently the maternal-infant bond is closely maintained in the first few hours after birth. Mothers may not depart to feed on the day of parturition, especially if birth has only taken place within a few hours of the emergence period. Observations made at Wilmore indicated that some mothers, having recently given birth, remained with their young until all other females had departed. Females may not depart until their newly-born offspring have been thoroughly groomed and the placenta has been discharged. This behavior also may reduce the chances of neonates being dislodged from roosts during emergence activity (Kunz, 1973).

I found no evidence that female *M. velifer* carried their newborn young while foraging, despite the fact that Twente (1955b) suggested that they may do so for the first few days. Of more than 1000 post-parturiant females trapped at colony entrances in the course of this study, only 12 were carrying young. In each instance, the circumstance could be accounted for by some previous disturbance (entry into the nursery area, banding, or handling young).

From birth until the age of six weeks, young bats undergo marked changes in behavior from a complete maternal dependence in the first day to complete independence at the age of six weeks. The curved, reticulated milk teeth, the well-developed claws on the hind feet and the first finger of newborn facilitate a tenacious attachment to their mother. In the first week, young usually occupy a place beneath their mother's wing. Because pelage of infants is still sparse and poorly developed, this behavior may be important in heat transfer from mother to infant. By the time young have become more densely furred (at the age of one to two weeks) they may hang beside their mothers or on her back.

INITIATION OF FLIGHT

Young *M. velifer* initiated flights within the confines of their roost at the age of three weeks. Simulated flight motions prior to this were made when individuals extended their wings laterally, forcing them in a down-stroke, and simultaneously lifting their bodies upward. Repetitive movements of this type were observed rather frequently. Young bats would hold a "stretch-and-push" position for nearly five seconds and repeat it up to six times within a period of a few minutes; concurrently they lifted their heads and opened their mouths as if they were echolocating. Gould (1971) observed this head-lifting behavior and sound emission and suggested that this motor pattern probably permitted young bats to test their physical surroundings before initiating flight.

Few young bats emerged on evening foraging flights before mid-

July, although a number of individuals began making short flights within the roost in the first week of July (Kunz, 1973). This pre-flight behavior was common prior to the time that young bats actually departed to feed and was characterized by straight-line flights (from two to five meters in distance). Individuals often shifted from one roost to another regaining altitude after initially dropping from their roost. Several days after straight-line flights were initiated some individuals began to make turning maneuvers and sustained flight for extended periods.

Flight not only depends on sufficient behavioral readiness but also on physical development. Because camber of the wing is produced by the flexion of the phalanges and particularly that of the fifth finger (Vaughan, 1959), flight efficiency and maneuverability would be expected to improve with physical maturation. One requirement of flight is the development of a wing surface that can be held rigidly against the force of an air stream (Vaughan, 1959, 1970). Therefore, until the fifth finger can be held in a stabilized position, the development of camber probably is one factor limiting early flight activity.

Wing-loading.—The fact that low wing-loading permits bats to fly at relatively low speeds is clearly advantageous to young in early stages of flight. The wing area of one to two-day old *M. velifer* is 10.75 cm^2 , which is approximately 10 percent of the adult wing area (Kunz, 1971). By the time young are three weeks of age the wing area is nearly 76 percent of adult size, and corresponds to the proportion of 76.6 percent given for *M. myotis* when flight was initiated at the age of three weeks (Krátky, 1970). By comparing wing-loading of pre-volant young with maximum adult wing-loading, it is evident that juveniles reach adult-like loading near the time they initiated flights within the roost (Fig. 10).

Although changes in body weight remain negligible from four to five weeks (Fig. 8), wing elements continue to increase in size after flight has been initiated (Fig. 7). This suggests that wing-loading will remain low, at least until fat deposition begins in late August. Because the wing area is directly correlated with the dimensions of the wing elements, the wing area would approach 96 to 98 percent of adult size at the age of 60 days. By selecting an average of 97 percent for the adult wing area (104 cm^2), and a mean body weight of juveniles at the age of 60 days (10.2 gm), juvenile wing-loading at this time would be approximately 0.97 gm/cm^2 . This value is considerably less than measures for pre-volant bats (Table 5) but closely approximates the wing-loading of adults taken in spring roosts (Kunz, 1971). Low wing-loading values up until this time, when young are developing flight proficiency and beginning to secure resources, would have an obvious selective advantage.

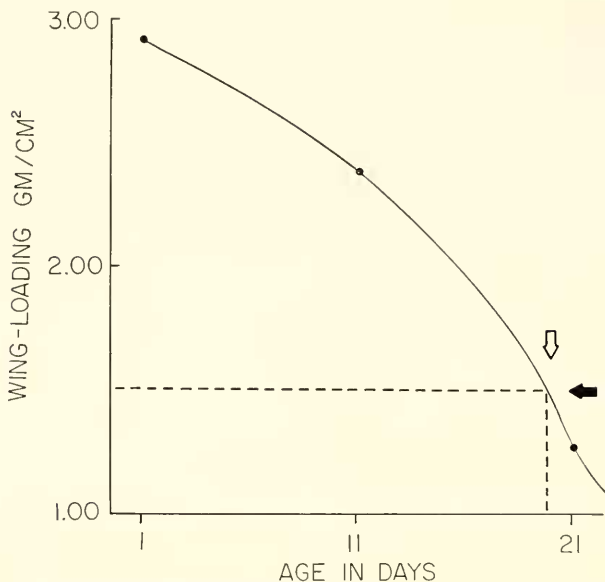


FIG. 10. Wing-loading of juvenile *M. velifer*. Maximum adult wing-loading is shown by the solid arrow, and the age at which adult-like wing-loading is achieved by juveniles is shown by the open arrow. The graph is based on data in table 5 and data for wing-loading computed for adults (Kunz, 1971).

INFANT MORTALITY

Infant mortality may be high during the first few days after birth. Before young have well developed motor coordination, some individuals may fall or be dislodged from their roost by older bats. Several dead and dehydrated young were found beneath the roost at Wilmore in the summer of 1969. Whether these individuals had died on impact, were stillborn, or were abandoned after unsuccessful attempts to retrieve them could not be determined; all appeared to be physically well formed.

Young that fall from their roosts may be susceptible to predation, drowning, or abandonment. At sites where nursery roosts are located over water (National Gypsum Mine), young that fall from the ceiling probably succumb. Young bats that fall into wet guano also may die before being retrieved. Only when areas beneath roosts are relatively dry, do neonates have a good chance of being recovered. In June 1970, I observed a neonate that had fallen to the floor at Wilmore from a height of approximately three meters. Soon afterward, an adult bat (presumed to be its mother) made several low, sweeping flights around the fallen young. She landed over it with her wings outstretched and after approximately three minutes flew

from the ground, returning the neonate to the roost above. Successful retrieval may depend in part on the size of infants and on their relative physical condition. Females may not be able to carry large young or those that are weak or injured and unable to assist in a retrieval.

Infant mortality is difficult to assess because an undetermined loss may result from predation. In the summers of 1969 and 1970, rat snakes (*Elaphe guttata*) were encountered in the nursery area at Lost Colony. Only in 1970 were snakes found that had actually eaten neonates that apparently had fallen to the floor of the cave. In each instance these observations were made soon after adults had departed to feed; perhaps these young were dislodged from their roost at the time of emergence activity.

DISCUSSION

Reproduction

MALES.—Judging from the changes in size of the epididymides and testes (Fig. 1), and observations in the field, copulation occurs mostly in September and October. Evidence that copulation had occurred by mid-October was based on the occurrence of a wet vaginal region or the occurrence of dried semen on the venter of females. Krutzsch (1961) noted that copulation in this species also may occur during wakeful periods in winter and it has been suggested that the intermittent activity in "warm rooms" of hibernacula (Twente, 1955b) may serve a reproductive function. The decrease in size of the epididymides throughout the winter supports these observations. Sperm resorption and tubular involution may account for some of the decrease in size in this period. Observations in spring suggest that some copulation occurs at this time. Guthrie (1933) observed copulations of *Myotis lucifugus* in spring, and Rice (1957) suggested that spring copulations in *Myotis austroriparius* may function to ensure the insemination of yearling females. Further studies are needed to detail the reproductive activity of male *M. velifer* and other species, especially upon arousal from hibernation.

The time required for the development of sexual maturity in males has not been widely studied. Apparently, *M. velifer* does not produce mature spermatozoa in their first autumn (Krutzsch, 1961). Christian (1956) indicated that male *Eptesicus fuscus* are sexually active in their first autumn although in other species, including *M. lucifugus* and *M. grisescens* (Miller, 1939), *Plecotus townsendii* (Pearson, *et al.*, 1952), *M. myotis* (Sluiter, 1961), individuals apparently do not become sexually mature until their second autumn. Fenton (1969b) observed young *M. lucifugus* copulating in autumn, but whether or not these copulations resulted in pregnancies was

undetermined. Studies where young bats can be marked soon after birth and later recovered and compared histologically are needed to detail sexual maturation in males.

The seasonal differences in sex ratios and the observed shift in the proportion of males at Lost Colony and Wilmore (Table 1) may be correlated with the onset of gonadal development in summer. It has been documented in other mammalian groups that spermatogenesis is retarded at high temperatures where a breakdown in important enzyme systems has been implicated (Glover and Young, 1963). Detrimental effects from exposure to high environmental temperatures in summer could interfere with spermatogenesis. Because spermatogenesis is sensitive to localized increases in temperature, solitary behavior and occupation of cooler caves could be an important reproductive strategy for males.

Data from the National Gypsum Mine indicate that adult males are less gregarious than females in summer, and furthermore, that most occupy relatively cooler roost sites than females. Body temperatures of males thus could potentially remain cooler than if they occupied active clusters or roosted in areas that were susceptible to high ambient temperatures. It is of interest that comparatively few males occupied the Wilmore barn which was subject to higher temperatures than at Lost Colony. Perhaps the existence of higher temperatures at Wilmore explains why proportionately more males departed from this site before they did from Lost Colony. If yearling males do not become sexually mature until their second autumn (Kruttsch, 1961) this might be explained, in part, by the fact that they do remain at nursery roosts throughout their first summer and are therefore exposed to higher temperatures.

Females.—The absence of differences in parturition dates or duration of lactation at Lost Colony and Wilmore (Fig. 6) suggests that factors influencing the timing of reproductive activity for these two nurseries in 1969 were similar. Both nurseries were occupied by approximately the same number of adult females in 1969, but the population at Lost Colony in late May and early June was larger than at Wilmore owing to the greater number of males (Table 1). Although this difference may only reflect the behavior of males in response to different thermal environments at this time of year, the presence of the larger total population at Lost Colony also may contribute to a greater increase in temperature at the cave than otherwise may be possible in the absence of males. Perhaps the presence of males is important initially to the successful occupation of a relatively cool cave in spring.

It has been demonstrated that low temperatures are capable of retarding embryonic development and extending the gestation period in bats (Eisentraut, 1937; Racey, 1969). Wimsatt (1969) noted that females may be more susceptible to cold depression in early

stages of pregnancy, and that lengthening of gestation may involve arresting early stages of embryonic development, rather than later when complex placental relationships have become established.

To assess the possible influence of environmental factors on gestation, I compared median parturition dates at Lost Colony and Wilmore in two different years. In 1969, the median parturition date at both nurseries was estimated to be 21 June (Fig. 6). Between 19 and 22 June 1970, samples again were taken at these two nurseries to compare with estimates for these dates in 1969. Of 356 females taken at Lost Colony on 21 June, only 90 (25.2%) were lactating, whereas at Wilmore on 19-20 June, only 68 (33.4%) of 215 females had given birth, revealing that gestation likely was longer at both sites in 1970 than in 1969 or that it began later in the spring.

When mean minimum ambient temperatures in April and May were compared for the two years, it was found that temperatures in early spring 1970 were slightly cooler than those in 1969. In April and May 1969, the mean minimum temperatures were 7.2° C and 13.2° C, respectively, and in April only one day was recorded as having a temperature below freezing. In spring 1970, the mean minimum temperatures for April and May, respectively, were 6.2° C and 13.4° C, and five days in April were recorded as having temperatures below freezing. The differences recorded in April were small but they may have been enough to account for the difference in gestation periods in the two years. The fact that there were five days in April 1970 where temperatures were recorded below 0° C may be the most important consideration.

When the 1970 percentages of post-parturiant females at Lost Colony and Wilmore are compared, the proportion of lactating females at the former (25.2%) is less than the proportion at Wilmore (33.4%). The fact that the sample at Lost Colony was taken a day later than that for Wilmore suggests that even fewer lactating females would have been found there had samples been taken on the same dates. Although the null hypothesis that there was no difference between these two percentages was accepted ($t=1.64$, $P>0.05$), the above data suggest that gestation may have been further delayed at Lost Colony. It is of interest that the population densities at each nursery in 1970 were reduced from their 1969 levels; the estimated population at Lost Colony in June 1970 was approximately 2000 adult females, compared to approximately 5000 in 1969 (Kunz, 1971). At Wilmore, the 1970 population also was lower than in 1969 but the reduction was less than at Lost Colony. Considering the fact that bats can increase the micro-temperature of their own roost and that populations in 1970 were reduced from the previous year, the size of the resident population may influence the duration of gestation.

Smith (1956) reported significant differences in the weight gains

of pregnant *Myotis lucifugus* in two different years. The fact that she found no correlation between ambient temperature and weight gain in the two years suggests that the observed difference in weight gain may be accounted for by the difference in population size in the two years of study (see Smith, 1954). Clustering behavior and maintenance of high metabolic levels usually are characteristic of females late in pregnancy (Smith, 1956; Stones and Wiebers, 1967). Herreid (1967) has shown that energy cost is less among individuals of *Tadarida brasiliensis* occupying large clusters than those in small clusters or singles. Perhaps when a nursery colony is reduced in size, and fewer bats are present to cluster, more energy is expended in maintaining homeothermy, and proportionately less is available for development. Additional studies involving examination of pregnant females in spring are needed to fully assess the influence of clustering behavior, population size, and ambient temperature on rates of gestation.

Daily production of milk probably reaches maximal levels in the second or third week following parturition and corresponds to the increasing size of the young and the increased food consumption at this time (Kunz, 1973). Davis *et al.* (1962) suggested that female *Tadarida brasiliensis* may produce an amount of milk equivalent to 16 per cent of their lactating body weight within a 24-hour period. Based on the 12 gram average weight of lactating *Tadarida* (Short, 1961), daily milk production per female should be in excess of 1.9 grams. Since Davis *et al.* (1962) also reported an average weight increase from daily food consumption of only one gram, there is little doubt that their estimation of milk production was too high or, alternatively, that their evaluation of food consumption was too low. Although I have no comparable data on milk production for *M. velifer*, my estimates on daily food consumption for lactating females (Kunz, 1973) suggest that their estimate of food consumption for *Tadarida* (a bat comparable in size to *M. velifer*) was much too low.

Growth and Development

Few studies provide data on growth of known-age bats under natural conditions. Because the forearm has been the most consistently measured element in growth studies, comparisons of the relative stages of development of several species were made at birth and at the age of six weeks to illustrate the similarity in growth. The forearm of *M. velifer* at birth and at six weeks are 34 and 96 percent, respectively, of adult size. Proportions based on data given for *Antrozous pallidus* (Davis, 1969) at birth and at six weeks are 32 and 96 percent, respectively. Corresponding values for *Plecotus townsendii* are 38 percent at birth and 98 percent at the age of six weeks (Pearson *et al.*, 1952). Similar proportions based on data presented by Krátky (1970) for *M. myotis* are 37 percent at birth

and 98 percent at six weeks. This evidence illustrates the similarity of developmental stages at the time of birth and at the time when young bats probably are weaned.

Pearson *et al.* (1952) reported an absolute growth rate of 0.55 mm per day for the forearm of *Plecotus townsendii* in the first 16 days of growth, and Davis *et al.* (1968) reported that some individual *Eptesicus fuscus* showed increases in forearm length in early stages of growth up to 2.6 mm per day. Based on data extrapolated from growth curves presented by the above authors, I have computed for comparison absolute growth rates for the forearm in the first 10 days. Rates of 1.20 mm per day for *Plecotus townsendii* and 1.45 for *Eptesicus fuscus* generally are comparable to the value of 1.56 determined for *M. velifer*.

At birth, the proportion of body weight of young to the weight of post-parturient female *M. velifer* (25.8%) closely approximates the proportions for *M. lucifugus* (24.6%) and *M. nigricans* (25.6%) recorded by Wimsatt (1960b) and Wilson (1971), respectively.

In the first two months of post-natal life, maximum body weight of *M. velifer* is attained at the age of three to four weeks. Loss of weight after this time seems to be common as it has been observed both in field and laboratory studies (Short, 1961; Kleiman, 1969; Davis, 1969; Krátky, 1970). Short suggested that this decrease may be accounted for by loss of body fats after young have become volant. The fact that similar decreases have been observed under conditions of laboratory confinement (Kleiman, 1969) suggests that nutritional conditions at time of weaning are important. Thus weight loss under natural conditions in this period may be accounted for by a combination of factors related to the weaning period and early flight activity, including reduced milk consumption, expenditure of accumulated fats, and inefficient insect capture (Kunz, 1973). Perhaps the deposition of fat in early developmental stages, and prior to the initiation of flight, is an important strategy that helps sustain juveniles through the weaning period.

Davis and Hitchcock (1965) observed that juvenile *M. lucifugus* continued to nurse after they had become volant and similar observations have been reported for *M. mystacinus* and *M. daubentoni* (Nyholm, 1965). The fact that volant young *M. velifer* contained both milk and the remains of insects (Kunz, 1973) suggests that weaning does not take place abruptly at the time young initiate foraging activity. Vocalizations that Gould (1971) recorded suggest that weaning may be initiated by the withdrawal behavior of young (weaning in *M. lucifugus* and *Eptesicus fuscus* apparently took place at the age of three weeks under conditions of laboratory confinement). Kleiman (1969) observed that weaning of *Eptesicus serotinus* and *Pipistrellus pipistrellus* in captivity began in the third or fourth week but was not completed until two to three weeks later.

Unusually long nursing periods have been reported for some bats reared in captivity (Eisentraut, 1936; Kleiman, 1969; and others). Differences in weaning time between captive bats and those under natural conditions may be due to artifacts resulting from nutritional deficiencies existing under laboratory confinement.

Juvenile *M. velifer* began feeding on insects near the time when permanent teeth were fully erupted (approximately 3-4 weeks); however, adult-like feeding behavior and success (Kunz, 1973) was not achieved until permanent teeth were fully developed (approximately 7-8 weeks). These observations are in contrast to those of Krátky (1970) who reported that permanent teeth in *M. myotis* were fully erupted in 30 days and that they did not begin to feed on insects until the age of 40 days (approximately 7 weeks). Continued linear growth and stabilization of body weight soon after foraging is initiated in *M. velifer*, results in a low wing-loading, and probably is important in leading to the development of successful feeding behavior.

Two generations of hair in the juvenile pelage were evident—over-hair, that began development in the prenatal period, and under-hair which appeared at approximately one week. A second generation apparently began as early as seven days as evidenced by darkening of the skin (melanin deposition).

A juvenile molt was initiated at approximately six weeks (when young bats had become nutritionally independent) and was not completed until September (10 weeks). These observations correspond to those reported by Mazák (1963) who noted that termination of hair growth in juvenile *M. myotis* coincided with the time that external measurements reached adult size.

Although parturition in this study occurred over a period of four weeks, there was no evidence of age segregation beyond the fact that the young less than two days old did not join older bats in forming clusters. The fact that juveniles less than two days of age were found scattered in peripheral areas suggests that either females intentionally deposit newborn young away from the densest part of the colony, or that the older young are more mobile and have a strong tendency to cluster. It seems likely that mothers would be able to locate their newborn easily if the latter were solitary, especially before the young have developed a reciprocal vocal response to their mothers' calls. Dwyer (1963) suggested that the behavior of females to deposit young on the periphery of nursery clusters may reduce the mortality of neonates by decreasing the probability of being dislodged by larger, more active individuals. Gould (1971) theorized that if bats remained organized into different age groups corresponding to the time of their birth, such behavior also may facilitate mothers recognizing their young as they returned from feeding.

Environment and Growth

Nursery sites that can be maintained at temperatures near thermal neutrality probably are important to the promotion of rapid growth in young. Also, less energy would be required for the maintenance of homeothermy at such temperatures. The selection of warm nursery roosts along with clustering behavior probably contribute measurably to a reduction in energy cost to individuals (Herreid, 1963, 1967). Cluster formation in nurseries not only provides a potential avenue for conductive and convective heat exchange for the enhancement of growth (Dwyer and Hamilton-Smith, 1965) but also in promoting efficient digestion and assimilation of food (Twente, 1955b; Davis *et al.*, 1962).

One of the initial designs of this study was to examine the relationships between growth and roost microclimate at Lost Colony and Wilmore. Efforts to obtain comparative temperature data at Lost Colony, however, were not completely successful. Measurements that were comparable are those from hygrothermograph records (Fig. 2). These data demonstrate that cave temperatures at Lost Colony remained near 20° C. Because bats at Lost Colony maintained high activity levels in daytime, I assumed that cluster temperatures (body surface temperatures), at least during and subsequent to parturition, would be similar to those recorded at Wilmore. If this assumption is valid, and individuals at Lost Colony had body temperatures in daytime between 32 and 37° C, body temperature-ambient temperature differentials would be expected to vary from 12-17° C. At Wilmore daytime differentials ranged from 5-12° C in the nursery period (see insert Fig. 3). If, on the average, higher temperature differentials are needed to maintain cluster temperatures at Lost Colony, then the energy cost of occupying Lost Colony would be greater than for occupying Wilmore. And, any difference in energy cost in occupying these two sites may be reflected in different growth rates, reproductive periods, or quantities of daily food consumption.

In spite of the apparent thermal differences at Lost Colony and Wilmore a seasonal comparison of reproductive parameters at these two sites (Fig. 6) suggests that there were no differences in reproductive chronology. The fact that parturition began at approximately the same time, the median parturition dates were the same and the lactation periods were comparable further suggests that post-natal growth rates may have been similar.

If early flight of young bats can be used as a measure of comparable growth, then I would suggest that there was no measurable difference in growth rates at these two nurseries in 1969. On 7-8 July and 8-9 July 1969, when young bats were first captured while departing to forage, approximately the same number of individuals was trapped at entrances in a comparable period or time; five were

taken at Lost Colony and six at Wilmore. Because both nurseries were occupied initially by the same number of young (approximately 5000), these data suggest that the same proportion of individuals in these two colonies reached flight stage at the same time. Mean forearm lengths of the earliest volant young trapped at Lost Colony (43.6 ± 0.56) and Wilmore (43.2 ± 0.70) are not significantly different ($t=0.54$, $P>0.05$).

Based on observations of Pearson *et al.* (1952) that *Plecotus townsendii* grew more rapidly at warmer temperatures, and the fact that Herreid (1963) recorded increases in cave temperatures throughout the nursery period, Herreid (1967) postulated that bats born in the early part of the parturition period would grow more slowly than those born later. To test this hypothesis groups of neonates that were born at Lost Colony both in the early and late stages of the parturition period were individually marked. One group consisted of individuals taken on 17 June, when approximately 300 (16% of the total juvenile population) had been delivered. The second group was taken on 27 June, after approximately 4500 (more than 90%) young were present. If growth rates differed according to the time of birth, I expected to find differences in the first three weeks since the most rapid growth occurs during this period (Fig. 8). Individuals marked as neonates on the above dates were recovered at intervals of 10 and 20 days after initial marking. Of all paired comparisons made (using a *t* test) no significant differences in linear size or weight were found ($P>0.05$). Although differences in growth may be evident in later periods, sample sizes (less than five on any one capture date) at these times were inadequate for making valid comparisons. Although these data fail to support the hypothesis presented by Herreid (1967), they do not disprove the premise that temperature may have a measurable effect on development.

Additional studies are needed to examine the influence of environmental factors and roost temperatures on growth and development of bats. Studies using the von Bertalanffy growth analysis (Fabens, 1965) may be useful for comparing growth patterns at different environmental temperatures. According to von Bertalanffy (1960), growth occurs most rapidly where protein turnover is high. Interspecific and intraspecific growth comparisons could be made by comparing catabolic constants in roosts subject to different thermal environments—the higher the catabolic constant, the faster the growth rate. The catabolic constant is determined as $3k$, where k is the intrinsic rate of growth (see Methods and Materials). An anabolic constant also may be computed (Fabens, 1965), but because it is a function of body weight, and computed curves may not correspond to observed measures, this determination may be less useful.

Geographic Variation

Bats occurring at northern latitudes and higher altitudes usually give birth later than do those in more southerly areas and at lower elevations. Differences in temperature, abundance of resources, and variation in periods of hibernation all have been implicated as influencing factors. Few studies on *M. velifer* are available that permit a broad geographic comparison of reproduction. Hayward (1970) assumed that the average birth date of populations in Arizona was 17 June, although he presented little evidence to substantiate his assumption. Davis *et al.* (1962), however, reported that parturition in *M. velifer* occurred several weeks before parturition of *Tadarida brasiliensis* in southern Texas. Examination of dates recorded for *Tadarida* would suggest that most of the births for *M. velifer* occurred in early June. This and the fact that young reportedly were flying in Texas by late June suggest that the average parturition period for that latitude was two to three weeks sooner than in Kansas. Owing to the wide distribution of *M. velifer* it would be of interest to compare reproduction in the northern populations with those occurring at lower latitudes, especially in areas where the availability of resources may be less influenced by thermal seasonality.

SUMMARY

A study detailing reproduction, growth and development of the cave bat, *Myotis velifer*, was conducted in south-central Kansas from March 1968 through January 1971. Reproductive and growth patterns were examined at two physically and thermally contrasting nurseries (barn and cave) that included a temporal analysis of gestation, parturition and lactation. Post-natal growth was determined from mark-recapture data. Reproductive activity of males was examined throughout an annual cycle.

Adult males and females occurred in approximately equal numbers at transient and nursery roosts in spring. By early June the adult sex composition at the nursery sites was predominantly female. A comparison of the sex composition of adults occupying a cave and a building revealed that proportionately fewer males occupied the building. These differences may be related to the intolerance of males for high roost temperatures in buildings.

Testes began increasing in size in June and reached maximum hypertrophy in late August. After late August and early September the testes decreased in size and remained in an arrested state until the following summer. In early autumn the epididymides increased in size and became maximally distended with spermatozoa by mid-October. Most copulations occurred in October.

Ovulation probably occurs in April when bats depart from hiber-

nacula. The gestation period was 60 to 70 days and most of the prenatal growth occurs in the latter three weeks of gestation. In 1969, parturition began in the second week of June and extended for approximately four weeks with a median parturition date of 21 June. Nearly 80 percent of all young were born in a two week period from mid to late June. Females apparently are reproductive in their first year with no significant tendency for them to give birth later than older females. No apparent differences in growth rates were evident in bats occupying a cave and a building nursery. A comparison of reproductive parameters at two sites in 1969 and 1970 revealed that parturition in 1970 was later than in 1969 suggesting that cooler temperatures and a reduced population size may have contributed to this observed difference.

Post-natal growth followed a decaying exponential model. The forearm and fifth finger lengths at birth were 34 and 29 percent of adult size, respectively. Growth occurred rapidly in the first three weeks in which time the above linear dimensions exceeded 80 percent of adult size. By the fourth week when young bats began to forage, the forearm had reached 90 percent of adult size. The fifth finger did not reach equivalent proportions until the fifth or sixth week. Adult linear size was achieved at the age of 9 to 10 weeks (late August and early September). Young bats at birth weighed 3.0 grams (25.8% of adults); by the time they were three weeks of age they exceeded 85 percent of adult weight. By the fourth week their weight stabilized between 82 and 86 percent of adult weight until fat deposition began in late August.

Flight was initiated within the confines of the nursery roost at the age of three weeks. When bats began to forage permanent teeth were fully erupted. Weaning occurred at approximately six weeks when linear dimensions had reached 90 percent of adult size. Juvenile pelage increased in density until the age of three to four weeks. A juvenile molt was initiated at the age of six weeks (when young became nutritionally independent) and was completed near the time that external measurements reached adult size.

The importance of clustering behavior and the maintenance of roost temperatures were discussed with respect to successful reproduction and growth.

APPENDIX

<i>Name</i>	<i>Coordinate (N, W)</i>	<i>County</i>
Belvidere (Barn)	37°30'35", 99°03'56"	Kiowa
Double Entrance S Cave	37°04'37", 99°02'25"	Comanche
Englewood (Barn)	37°07'30", 100°03'03"	Clark
Lost Colony Cave	37°01'46", 98°59'06"	Barber
National Gypsum Mine	37°21'46", 98°56'47"	Barber
Protection (Barn)	37°03'28", 99°28'53"	Comanche
Wilmore (Barn)	37°19'37", 99°09'16"	Comanche

LITERATURE CITED

- ASDELL, S. A.
1964. Patterns of mammalian reproduction. Cornell Univ. Press, Ithaca, New York, 2nd ed., 670 pp.
- BARBOUR, R. W., and W. H. DAVIS
1969. Bats of America. Univ. Press of Kentucky, Lexington, 286 pp.
- CARTER, D. C.
1970. Chiropteran reproduction. Pp. 233-246, in About bats (B. H. Slaughter and D. H. Walton, eds.), Southern Methodist Univ. Press, Dallas.
- CHRISTIAN, J. J.
1956. The natural history of a summer aggregation of the big brown bat, *Eptesicus fuscus fuscus*. Amer. Midland Nat., 55:66-95.
- CONSTANTINE, D. G.
1957. Color variation and molt in *Tadarida brasiliensis* and *Myotis velifer*. J. Mamm., 38:461-466.
- DAVIS, R.
1969. Growth and development of young pallid bats, *Antrozous pallidus*. J. Mamm., 50:729-736.
1970. Carrying of young by flying female North American bats. Amer. Midland Nat., 83:186-196.
- DAVIS, R. B., C. F. HERREID, II, and H. L. SHORT
1962. Mexican free-tailed bats in Texas. Ecol. Monogr., 32:311-346.
- DAVIS, W. H., and H. B. HITCHCOCK
1965. Biology and migration of the bat, *Myotis lucifugus*, in New England. J. Mamm., 46:296-313.
- DAVIS, W. H., R. W. BARBOUR, and M. D. HASSELL
1968. Colonial behavior of *Eptesicus fuscus*. J. Mamm., 49:44-50.
- DUNNIGAN, P. B., and J. H. FITCH
1967. Seasonal movements and population fluctuations of the cave bat (*Myotis velifer*) in south-central Kansas. Trans. Kansas Acad. Sci., 70:210-218.
- DWYER, P. D.
1963. The breeding biology of *Miniopterus schreibersi blepotis* (Temminck) (Chiroptera) in northeastern New South Wales. Australian J. Zool., 11:219-240.
1966. The population pattern of *Miniopterus schreibersii* (Chiroptera) in north-eastern New South Wales. Australian J. Zool., 14:1073-1137.
- DWYER, P. D., and E. HAMILTON-SMITH
1965. Breeding caves and maternity colonies of the bent-winged bat in south-eastern Australia. Helictite, 4:3-21.
- EISENTRAUT, M.
1936. Zur Fortpflanzungsbiologie der Fledermäuse. Zeit. Morph. Okol. Tiere, 31:27-63.
1937. Die Wirkung niedriger temperaturen auf die Embryonale Entwicklung bei Fledermäusen. Biol. Sentralblatt. Leipzig, 57:59-74.
- FABENS, A. J.
1965. Properties and fitting of the von Bertalanffy growth curve. Growth, 29:265-289.
- FENTON, M. B.
1969a. The carrying of young by females of three species of bats. Canadian J. Zool., 47:158-159.
1969b. Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. Canadian J. Zool. 47:597-602.

1970. The deciduous dentition and its replacement in *Myotis lucifugus* (Chiroptera: Vespertilionidae). Canadian J. Zool., 48:817-820.
- GLOVER, T. D., and D. H. YOUNG
1963. Temperature and the production of spermatozoa. Fertil. Steril., 14:441-450.
- GOULD, E.
1971. Studies of maternal-infant communication and development of vocalizations in the bats *Myotis* and *Eptesicus*. Comm. Behav. Biol. (Part A), 5:263-313.
- GRIFFIN, D. R.
1940. Notes on the life history of New England bats. J. Mamm., 21:181-187.
- GUTHRIE, M. J.
1933. The reproductive cycle of some cave bats. J. Mamm., 14:199-216.
- HAYWARD, B. J.
1970. The natural history of the cave bat *Myotis velifer*. Res. Sci., Western New Mexico Univ., 1:1-74.
- HERREID, C. F., II
1963. Temperature regulation of Mexican free-tailed bats in cave habitats. J. Mamm., 44:560-573.
1967. Temperature regulation, temperature preference and tolerance, and metabolism of young and adult free-tailed bats. Physiol. Zool., 40:1-22.
- HUMPHREY, S. R.
1971. Population ecology of the little brown bat *Myotis lucifugus*, in Indiana and north-central Kentucky. Ph.D. dissertation, Oklahoma State Univ., 138 pp.
- KLEIMAN, D. G.
1969. Maternal care, growth rate and development in the noctule (*Nyctalus noctula*), pipistrelle (*Pipistrellus pipistrellus*) and serotine (*Eptesicus scrotius*) bats. J. Zool., 157:187-211.
- KRÁTKÝ, J.
1970. Postnatale Entwicklung des Grossmausohrs, *Myotis myotis* (Borkhausen, 1797). Vest. Českoslov. Spol. Zool., 33:202-218.
- KRUTZSCH, P. H.
1961. The reproductive cycle in the male vespertilionid bat *Myotis velifer*. Anat. Rec., 139:309 (abstract).
- KUNZ, T. H.
1971. Ecology of the cave bat, *Myotis velifer*, in south-central Kansas and northwestern Oklahoma. Ph.D. dissertation. The University of Kansas, 148 pp.
1973. Feeding ecology of a temperature insectivorous bat (*Myotis velifer*). M.S. submitted for publication.
- LAIRD, A. K.
1966. Postnatal growth of birds and mammals. Growth, 30:349-363.
- LAIRD, A. K., S. A. TYLER, and A. D. BARTON
1965. Dynamics of normal growth. Growth, 29:233-248.
- MAZÁK, V.
1963. Hair growth in large mouse-eared bat, *Myotis myotis myotis* Borkhausen, 1797 (Mammalia, Chiroptera), during its prænatal and early postnatal life. Vest. Českoslov. Spol. Zool., 27:234-242.
- MILLER, G. S., JR., and G. M. ALLEN
1928. The American bats of the genera *Myotis* and *Pisonyx*. Bull. U.S. Natl. Mus., 144:viii+218 pp.

MILLER, R. E.

1939. The reproductive cycle in male bats of the species *Myotis lucifugus* and *Myotis grisescens*. J. Morph., 64:267-295.

NYHOLM, E. S.

1965. Zur Ökologie von *Myotis mystacinus* (Leisl.) und *M. daubentoni* (Leisl.) (Chiroptera). Ann. Zool. Fenn., 2:77-123.

ORR, R. T.

1970. Development: Prenatal and Postnatal. pp. 217-231, in Biology of bats (W. A. Wimsatt, ed.), Vol. 2, Academic Press, New York.

PEARSON, O. P., and M. R. KORFORD, and A. K. PEARSON

1952. Reproduction of the lump-nosed bat (*Corynorhinus rafinesquei*) in California. J. Mamm., 33:273-320.

RACEY, P. A.

1969. Diagnosis of pregnancy and experimental extension of gestation in the pipistrelle bat. J. Reprod. Fertil., 19:465-474.

RICE, D. W.

1957. Life history and ecology of *Myotis austroriparius* in Florida. J. Mamm., 38:15-32.

ROER, H.

1968. Nehmen die Weibchen des Mausohrs, *Myotis myotis* (Borkhausen), ihr Neugeborenes auf ihren Nahrungsflügen mit? Zeit. Tierpsychol., 25:701-709 (English summary).

ROER, H., and W. ECSBAEK

1969. Über die Balz der Wasserfledermaus (*Myotis daubentoni*) (Chiroptera) in Winterquartier. Lynx, 10:85-91 (English summary).

SHORT, H. L.

1961. Growth and development of Mexican free-tailed bats. Southwestern Nat., 6:156-163.

SLUITER, J. W.

1961. Sexual maturity in males of the bat *Myotis myotis*. Proc. Kon. Ned. Akad. Wet., Amsterdam, C, 64:243-249.

SMITH, E.

1954. Studies on the life history of non-cave dwelling bats in northeastern Ohio. Ohio J. Sci., 54:1-12.

1956. Pregnancy in the little brown bat. Amer. J. Physiol., 185:61-64.

STONES, R. C., and J. E. WIEBERS

1967. Temperature regulation in the little brown bat. *Myotis lucifugus*. Pp. 97-109, in Mammalian hibernation III (K. C. Fisher *et al.*, ed.), American Elsevier, New York.

TINKLE, D. W., and W. W. MILSTEAD

1960. Sex ratios and population density in hibernating *Myotis*. Amer. Midland Nat., 63:327-334.

TINKLE, D. W., and I. G. PATTERSON

1965. A study of hibernating populations of *Myotis velifer* in northwestern Texas. J. Mamm., 46:612-633.

TWENTE, J. W., JR.

- 1955a. Aspects of a population study of cavern-dwelling bats. J. Mamm., 36:379-390.

- 1955b. Some aspects of habitat selection and other behavior of cavern dwelling bats. Ecology, 36:706-732.

VAUGHAN, T. A.

1959. Functional morphology of three bats: *Eumops*, *Myotis*, *Macrotus*. Univ. Kansas Publ., Mus. Nat. Hist., 12:1-153.

1970. Flight patterns and aerodynamics. Pp. 195-216, in Biology of bats (W. A. Wimsatt, ed.), vol. 1, Academic Press, New York.

VON BERTALANFFY, L.

1960. Principles and theory of growth, Pp. 137-259, in *Fundamental aspects of normal and malignant growth* (W. W. Nowinski, ed.), Elsevier Publ. Co., Amsterdam.

WILSON, D. E.

1971. Ecology of *Myotis nigricans* (Mammalia: Chiroptera) on Barro Colorado Island, Panama Canal Zone. *J. Zool.*, 163:1-13.

WIMSATT, W. A.

1944. Growth of the ovarian follicle and ovulation in *Myotis lucifugus*. *Amer. J. Anat.* 74:129-159.
1945. Notes on breeding behavior, pregnancy, and parturition in some vespertilionid bats of the eastern United States. *J. Mamm.*, 26:23-33.
- 1960a. An analysis of parturition in Chiroptera, including new observations on *Myotis l. lucifugus*. *J. Mamm.*, 41:183-200.
- 1960b. Some problems of reproduction in relation to hibernation in bats. *Bull. Mus. Comp. Zool.*, 124:249-267.
1969. Some interrelations of reproduction and hibernation in mammals. Pp. 511-549, in *Dormancy and survival* (H. W. Woolhouse, ed.), Academic Press, New York.